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Strontium and Oxygen Isotope Profiles of Sequentially Sampled Modern Bison (*Bison bison bison*) Teeth from Interior Alaska as Proxies of Seasonal Mobility

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ABSTRACT. Studies addressing prehistoric mobility in animals typically use isotopic analyses of sequentially formed tissues, such as the growth layers in teeth, to infer physical movement on the landscape. Strontium isotope ratios ($^{87}Sr/^{86}Sr$ values), which vary geographically, are particularly useful for this purpose, especially when paired with stable oxygen isotope ratios ($\delta^{18}O$), which vary seasonally. Together, these two isotope systems can provide information about past animal movement patterns on a seasonal scale. However, while many studies have used $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values from analyses of sequentially formed tissues for this purpose, there have been limited analyses on modern animals of known movement patterns across high-latitude regions. In this pilot study, we sequentially sampled and analyzed one second molar (M_2) and two third molars (M_3) from two bison (*Bison bison bison*) from the Delta bison herd, which resides in interior Alaska and has known and documented seasonal mobility patterns. The resulting $^{87}Sr/^{86}Sr$ values from the teeth were compared to a high-resolution $^{87}Sr/^{86}Sr$ isoscape for the region and were paired with $\delta^{18}O$ analyses to determine whether the seasonal $^{87}Sr/^{86}Sr$ values matched the predicted values for each of the seasonal bison habitat areas. The results indicate that the $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values reliably reflected the known seasonal mobility patterns of bison and suggest that this approach could be used to investigate the mobility patterns of prehistoric bison in Alaska and surrounding high-latitude regions.

Key words: bison; strontium isotopes; sequential sampling; behavioral ecology; mobility; Interior Alaska study

RÉSUMÉ. En général, les études qui portent sur la mobilité des animaux préhistoriques se servent d'analyses isotopiques des tissus séquentiellement formés, y compris les couches de développement des dents, afin d'en déduire les mouvements physiques dans l'environnement. Les rapports isotopiques du strontium ($^{87}Sr/^{86}Sr$) sont particulièrement utiles à cette fin, car ils varient géographiquement, surtout lorsqu'ils sont jumelés avec les rapports isotopiques stables de l'oxygène ($\delta^{18}O$), dont la variabilité est saisonnière. Ensemble, ces deux isotopes peuvent fournir des informations sur les habitudes de déplacement des animaux dans un paysage en fonction des saisons. Cependant, même si plusieurs études ont utilisé les valeurs $^{87}Sr/^{86}Sr$ et $\delta^{18}O$ découlant des analyses des tissus séquentiellement formés à cette fin, peu d'analyses ont été effectuées chez les animaux modernes dont les habitudes de déplacement sont connues dans les régions de haute latitude. Dans cette étude pilote, nous avons séquentiellement échantillonné et analysé une deuxième molaire (M_2) et deux troisièmes molaires (M_3) de deux bisons (*Bison bison bison*) du troupeau de bisons du delta, troupeau qui réside dans l'intérieur de l'Alaska et dont les modèles de mobilité saisonnière sont connus et documentés. Les valeurs $^{87}Sr/^{86}Sr$ obtenues à partir des dents ont été comparées à un paysage isotopique de haute résolution $^{87}Sr/^{86}Sr$ pour la région et ont été jumelées aux analyses $\delta^{18}O$ pour déterminer si les valeurs $^{87}Sr/^{86}Sr$ saisonnières correspondaient aux valeurs prévues pour les zones d'habitat saisonnières du bison. Les résultats indiquent que les valeurs $^{87}Sr/^{86}Sr$ et $\delta^{18}O$ reflètent fidèlement les modèles connus de mobilité saisonnière du bison, et suggèrent que cette méthode pourrait servir à étudier les modèles de mobilité des bisons préhistoriques en Alaska et dans les régions de haute latitude environnantes.

Mots clés : bison; isotopes du strontium; échantillonnage séquentiel; écologie comportementale; mobilité; étude de l'intérieur de l'Alaska

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INTRODUCTION

Studies in archaeology, paleoecology, and paleontology are uniquely suited to address long-term temporal changes in animal behavioral ecology that are not evident in modern datasets. These studies can provide vital information about how modern animal populations may respond to climate change in the future. Isotopic analyses have become essential for understanding the behavioral dynamics of both past and present organisms and are especially useful for paleo-studies because they provide information about past behavior that would be difficult to address through other means. Reconstructing the mobility patterns of extinct or prehistoric species can be especially challenging because the physical characteristics of skeletal tissues can provide only limited information. Direct biosignature studies, such as isotopic analyses, are one way to address these less tangible aspects of animal behavioral ecology. Sequentially formed osseous tissue, such as dental enamel, records changes in environmental isotope values over short periods of growth and development (on the scale of months or seasons), which can then be used to infer mobility and movement patterns in animals (e.g., Koch et al., 1989; Fricke and O'Neil, 1996; Sharp and Cerling, 1998; Gadbury et al., 2000; Bocherens et al., 2001; Balasse et al., 2002; Passey and Cerling, 2002).

Sequential sampling methods on dentition have been applied to many paleo-studies investigating seasonal mobility patterns of herbivores in North America, Europe, and Africa (e.g., Fricke et al., 1998; Hoppe et al., 1999, 2004; Gadbury et al., 2000; Balasse et al., 2002; Widga, 2006; Pellegrini et al., 2008; Fenner, 2009; Feranec et al., 2009; Graves, 2010; Britton et al., 2011; Julien et al., 2012, 2015). The reliability of these methods has also been demonstrated on modern species of *Rangifer* (Britton, 2009; Britton et al., 2009; Drucker et al., 2012; Price et al., 2015), *Bison* (Britton, 2009), and *Antilocapra* (Fenner and Frost, 2009). However, growth and development vary across species (e.g., Higgins and MacFadden, 2004; Feranec et al., 2009; Britton, 2009), and behavioral ecology within a single species can vary because of constraints in the species' physical environment (e.g., MacArthur, 1984; Johnson et al., 2001; Gates et al., 2010; Plumb et al., 2014). Therefore, more studies on modern animals are needed, particularly in regions such as the circumpolar North that experience large shifts in climate and seasonality (e.g., Fricke et al., 1998), or in species such as bison that have highly variable behavior (e.g., Plumb et al., 2014). Additionally, work by Douglas et al. (2013) has indicated that watershed $^{87}Sr/^{86}Sr$ values can fluctuate seasonally in areas of permafrost because of changes in hydrological sources and output between summer and winter seasons. This factor could be problematic for mobility studies in high-latitude regions because seasonal fluctuations in $^{87}Sr/^{86}Sr$ values could skew migratory signatures. However, animals that are not water-dependent (i.e., that derive their water from food sources), such as bison (Hoppe, 2006), would be less affected by this seasonal hydrological fluctuation in $^{87}Sr/^{86}Sr$ values.

This pilot study explores whether time-series profiles of strontium ($^{87}Sr/^{86}Sr$) and stable oxygen isotope ratios (expressed as $\delta^{18}O$ values) from sequentially sampled bison teeth can serve as a proxy of seasonal mobility patterns for modern bison in a high-latitude subarctic environment. Bison were widespread throughout Alaska for thousands of years and are considered an important species from both paleoecological (e.g., Guthrie, 1990) and archaeological (e.g., Potter et al., 2013) perspectives. Isotopic studies addressing prehistoric bison behavioral ecology and environmental proxies could provide significant information about past ecosystem dynamics; however, we must first establish the reliability of these methods for modern herds before applying them to prehistoric bison in Alaska or other circumpolar regions.

Previous work on modern bison (*Bison bison bison*) in mid-latitude regions of the western United States has indicated that $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values from sequentially sampled dental enamel correspond with expectations about broad seasonal movement patterns (Britton, 2009), but it is unknown whether the methods are reliable in high-latitude regions such as the subarctic, where seasonal hydrological variability could alter migratory signatures (e.g., Douglas et al., 2013). To address this issue, we sequentially sampled three molars from two individual bison of the Delta bison herd, which resides near Delta Junction, Alaska, and has documented seasonal mobility patterns, and analyzed the samples for $\delta^{18}O$ and $^{87}Sr/^{86}Sr$. We then compared the results to a high-resolution predictive model of $^{87}Sr/^{86}Sr$ variability for the region (Bataille et al., 2014). While this pilot study is limited to two individuals and likely does not capture the full range of behavior or physiological differences that would be displayed at the herd level, we feel that the sample is sufficient as a pilot study to address our primary goals, which include assessing the reliability of using time-series profiles of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values to reconstruct seasonal mobility patterns of modern bison and evaluating whether these methods would be reliable for studies of prehistoric bison behavioral ecology in high-latitude environments.

BACKGROUND

Ungulate Tooth Development

Dental enamel is a preferred tissue for isotopic studies because its dense crystalline structure makes it one of the best-preserved osseous tissues and least susceptible to contamination (Lee-Thorp et al., 1989; Wang and Cerling, 1994; Zazzo et al., 2005; Koch, 2007). Time-series methods are often applied to hypsodont dentition because the teeth grow in sequentially mineralized layers and are large enough to allow for collecting multiple samples along one or more of the lateral surfaces (Brown et al., 1960; Fricke

and O'Neil, 1996; Gadbury et al., 2000). As a tooth forms, elements (such as strontium and oxygen) are incorporated into the bioapatite portion of the tooth as it mineralizes, and their values do not change once the bioapatite has fully hardened (Bryant et al., 1996). Analyzing the isotope values from individual mineralized layers within a tooth essentially provides a "window" into a specific period of growth and development. Multiple sequential samples taken along the transverse plane of a tooth can reveal changes in the isotope values over time on the scale of seasons (Bryant et al., 1996; Fricke and O'Neil, 1996; Wiedemann et al., 1999; Gadbury et al., 2000; Balasse et al., 2002; Passey and Cerling, 2002; Zazzo et al., 2005).

Lower second and third molars (M_2 and M_3) are typically chosen for time-series studies because they have the longest period of development and capture approximately a year's worth of growth in most ungulate species (c.f., Fricke et al., 1998). In bison, M_2s begin forming about eight weeks after birth and complete their formation around the 13th month of life, encompassing about 11 months of growth, M_3s begin forming around the ninth month of life, and complete formation around the 24th month, encompassing about 15 months of growth (Brown et al., 1960; Gadbury et al., 2000). Because bison exhibit reproductive synchronicity—that is, calves are often born in the spring (Berger and Cunningham, 1994)—tooth eruption and growth can be correlated with specific times of the year. Maximum length for the enamel portion of bison molars has been reported as 63.4 mm for M_2s and 67.8 mm for M_3s (Niven and Hill, 1998; Widga, 2006), but tooth length is likely variable at both the individual and herd levels.

While the lengths and rates of tooth growth are well known, the process of enamel mineralization is complicated and only partially understood for many species. Mineralization occurs in several multi-directional phases (Suga et al., 1970; Suga, 1982), and it takes several months for the enamel to fully mineralize. Although an enamel sample from a certain location on a tooth correlates to a specific period of growth, the isotope values from that sample represent a range of homogenized values from a much longer time period associated with the enamel mineralization phase. In other words, there are two scales of time operating on samples of enamel. The location from which a sample is removed relates to physical growth and can be associated with a rough calendrical date; however, the isotope values from the sample do not relate to the same discrete period of time, but cover a much longer mineralization period, during which the enamel is still incorporating environmental isotopic signals. For bovid species, this mineralization process takes approximately six months and results in an isotopic signal that is attenuated by an estimated 10%–70% (Balasse, 2002, 2003; Kohn et al., 2002; Passey and Cerling, 2002; Hoppe et al., 2004; Kohn, 2004; Zazzo et al., 2005; Montgomery et al., 2010; Balasse et al., 2012). Because of this attenuation, changes in surrounding environmental isotope values will be reflected in the tooth isotopic profiles with respect to the duration of time spent in that environment; for example, a small change in values over a long period will be more visible than a large change in values over a short period (Zazzo et al., 2012). Another complication is that mineralization is not constant throughout a tooth, with the upper crown and mesial portions mineralizing faster than the lower portions and buccal or lingual sides (Jordana and Köhler, 2011; Zazzo et al., 2012; Bendrey et al., 2015). However, this issue may be minimal for bovid species: Hillson (2005) notes that striae of Retzius in cattle teeth are regularly spaced along the tooth crown, which suggests a relatively constant rate of growth (Montgomery et al., 2010). Additionally, it is not clear whether all isotopes mineralize at the same rate, or if the various isotopes have different rates of mineralization (e.g., Kohn et al., 2002; Montgomery et al., 2010). More studies on species-specific formation of dental tissue are needed to fully understand this complicated process, but are outside of the scope of this study.

Strontium and Oxygen Isotopes

Two isotope systems frequently used to examine mobility patterns are strontium and oxygen isotopes (Ericson, 1985; Sealy et al., 1995; Gat, 1996; Beard and Johnson, 2000; Bowen et al., 2005; Hobson et al., 2010). Strontium isotope ratios are especially useful for reconstructing geographical movement because $^{87}Sr/^{86}Sr$ values vary across the landscape as a function of the chemical composition, weathering rates, and age of the underlying geologic substrate, and these isotopes are incorporated into osseous tissues from food and water sources (Ericson, 1985; Sealy et al., 1995; Price et al., 2002; Bentley, 2006). Because strontium is relatively "heavy" (i.e., has a relatively high atomic mass), there is no measurable fractionation between environmental $^{87}Sr/^{86}Sr$ values and their values in osseous tissue (Bentley, 2006). This fact allows for a 1:1 correlation between the values from skeletal tissue and the values in the geographic area (i.e., surface soils) where the organism lived during the period when the tissue was forming. One caveat to $^{87}Sr/^{86}Sr$ studies of mobility is that the method can be applied only to species with large enough habitat areas to encompass regional $^{87}Sr/^{86}Sr$ variability that is greater than possible measurement error or attenuation due to sampling methods.

Isoscapes, which are predictive models of isotope variation, are often used for migration studies and can provide expectations for how isotope values may vary across a landscape. For $^{87}Sr/^{86}Sr$ values, this modeling has been accomplished in the past by modeling variation on the basis of underlying bedrock lithologies (e.g., Beard and Johnson, 2000; Bentley, 2006; Hobson et al., 2010; Bataille et al., 2014). However, bioavailable $^{87}Sr/^{86}Sr$ values (e.g., surface soils) can differ from the underlying geologic substrate, especially in large basins or river valleys, as a result of alluvial or aeolian transport of material from other sources (Bentley, 2006). This issue can be reduced by sampling plants, or fauna that have small habitat ranges, from the local environment for $^{87}Sr/^{86}Sr$ values, which can

provide a more accurate baseline for modeling the range of variation (e.g., Price et al., 1994). However, such sampling was outside of the scope of this study, and we relied on the isoscape generated by Bataille et al. (2014).

Studies that address mobility through sequential $^{87}Sr/^{86}Sr$ profiles often incorporate $\delta^{18}O$ values from analyses of the same tissues (e.g., Balasse et al., 2002; Pellegrini et al., 2008; Britton et al., 2009; Graves, 2010; Widga et al., 2010; Julien et al., 2012; Fisher and Valentine, 2013). Variability in $\delta^{18}O$ values from skeletal tissues is related to hydroclimatic changes and can be used to characterize seasonal as well as altitudinal variation in sequentially sampled tissues (Koch et al., 1989; Fricke and O'Neil, 1996; Gat, 1996; Fricke et al., 1998). Mid- and high-latitude regions demonstrate seasonal fluctuations in $\delta^{18}O$ values related to rain vs. snowfall (Fricke and O'Neil, 1996; Gat, 1996). When this variation is plotted, it represents a sinusoidal wave with $\delta^{18}O$ values that are lower in the winter than in the summer (e.g., Fricke et al., 1998; Bernard et al., 2009; Feranec et al., 2009; Julien et al., 2012). When $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ values from the same sequentially sampled tissue are compared, it is possible to correlate physical movement patterns (based on the $^{87}Sr/^{86}Sr$ values) with summer and winter seasons (based on the peak high and low $\delta^{18}O$ values).

Previous Studies of Seasonal Mobility

Time-series profiles of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values from dental enamel have been used to investigate many aspects of prehistoric ungulate behavioral ecology, including seasonal mobility and dietary habits of Pleistocene-aged steppe bison (*Bison priscus*) in Ukraine (Julien et al., 2012); seasonal mobility patterns of Pleistocene-aged horse (*Equus hydruntinus*) and red deer (*Cervus elaphus*) in Italy (Pellegrini et al., 2008); seasonal mobility patterns in Pleistocene-aged caribou (*Rangifer tarandus*) and bison (*Bison priscus*) in Europe (Britton, 2009; Britton et al., 2011; Price et al., 2017); mobility, diet, and behavioral changes of bison (*Bison bison*) on the Great Plains during the Holocene (Widga, 2006; Graves, 2010; Widga et al., 2010); changes in the habitats of mountain sheep (*Ovis canadensis*) in the Great Basin during the Holocene (Fisher and Valentine, 2013); and domestication of sheep (*Ovis aries*), cattle (*Bos taurus*), and horse (*Equus caballus*) throughout Europe during the Holocene (Balasse et al., 2006; Balasse and Tresset, 2007; Bendrey et al., 2009; Henton et al., 2010; Towers et al., 2010).

Although these methods have been applied to a range of species across mid-latitude regions, these studies are complicated by the nature of tooth growth and development, species-specific variability, or changes in environmental predictability such as periods of rapid climate change (e.g., the Pleistocene-Holocene transition). Most studies that have evaluated these methods using modern animals have focused on understanding tooth growth and development in domesticated animals such as sheep, horses, and cattle from mid-latitude regions (Balasse et al., 2002, 2012; Passey and Cerling, 2002; Balasse, 2003; Higgins and MacFadden, 2004; Hoppe et al., 2004; Nelson, 2005; Zazzo et al., 2010, 2012; Towers et al., 2014; Bendrey et al., 2015). These studies have demonstrated the complex nature of tooth growth and development and elucidated many aspects of using isotopes from sequentially sampled dentition as environmental and behavioral proxies. However, more studies are needed on wild herds and in high-latitude regions, such as the subarctic.

One exception to the focus on mid-latitude studies is the seminal work by Britton et al. (2009), which used time-series profiles of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values from the teeth of five modern caribou (*Rangifer tarandus granti*) from the North Slope of Alaska to test whether the measured values reflected the known seasonal migration patterns of the herd and matched the expected $^{87}Sr/^{86}Sr$ values for the seasonal habitats. Portions of the herd had been radio-collared and tracked for several decades, providing precise information about seasonal migration patterns. Expectations about regional variability in $^{87}Sr/^{86}Sr$ values were based on soil samples from previous studies and known regional bedrock lithology, but these values were not modeled as an isoscape. Migratory signatures were determined by comparing the $^{87}Sr/^{86}Sr$ values of the five teeth, which showed variation in the second or third decimal place for four of the individuals and matched the expectations of the $^{87}Sr/^{86}Sr$ regional variability for the known seasonal movement patterns. The work of Britton et al. (2009) indicated that this method can be a reliable proxy for identifying seasonal migration of caribou herds and is the only study that has investigated these methods for modern species in a high-latitude environment. Importantly, this work has provided expectations for our own study, and provides a point of comparison for modern ungulate species in Alaska.

Another study that has helped to validate sequential sampling methods in modern wild herds was conducted by Britton (2009) on five bison from herds located in South Dakota, Utah, and Oklahoma. Three of the individuals, from the Henry Mountains herd in Utah and the Wichita Mountains herd in Oklahoma, lived in regions of homogenous geology, while the other two, from the Wind Cave herd in South Dakota, lived in a region with variable geology. That study explored whether the seasonal $^{87}Sr/^{86}Sr$ values for the five individuals would reflect their respective geologic environments. While the methods used were similar to those of Britton et al. (2009), the seasonal mobility patterns of these bison had not been closely tracked: general information about their movement patterns was known, but no radio-collars or close monitoring was available. Expectations about the $^{87}Sr/^{86}Sr$ variability in the different habitats were based on regional bedrock lithology, and seasonal migratory signatures were identified through variation in the $^{87}Sr/^{86}Sr$ values of the five teeth and comparison with $\delta^{18}O$ values. The results demonstrated that the $^{87}Sr/^{86}Sr$ values from the teeth corresponded with the expectations about the geologic variability in the different bison habitats. The three bison that lived in regions of

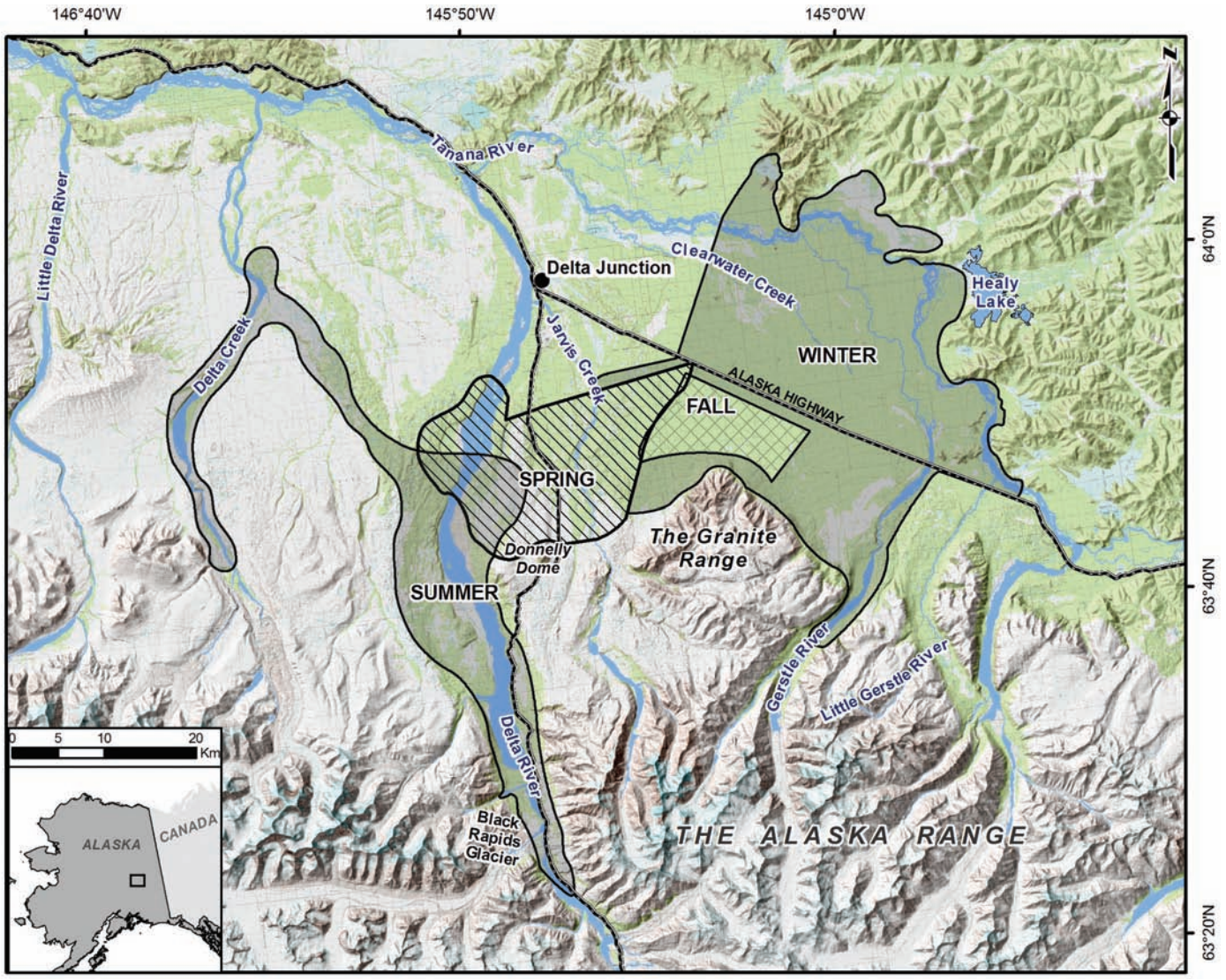

FIG. 1. Seasonal ranges of the Delta bison herd. The summer range encompasses upland areas of the Delta River and Little Delta Creek basins, while the winter range encompasses lowland areas along the Tanana River, the lower Gerstle River, and tributaries. The fall range is nearly identical to the winter range, except for a small area along the base of the Granite Range, between Jarvis Creek and the Gerstle River, where the bison congregate for mating season. The spring range encompasses an upland area near Donnelly Dome, midway between the summer and winter ranges.

homogenous geology showed little variation in $^{87}Sr/^{86}Sr$ values during different seasons, while the two bison that lived in a region with more variable geology showed greater variation in $^{87}Sr/^{86}Sr$ values (Britton, 2009). Our work builds on this previous research and tests the reliability of using sequential-sampling methods to examine mobility patterns of bison in high-latitude regions by incorporating well-documented movement patterns and a high-resolution $^{87}Sr/^{86}Sr$ isoscape (Bataille et al., 2014).

THE DELTA BISON HERD

History of the Herd

This pilot study used tooth specimens from the Delta bison herd, which resides near Delta Junction, Alaska. No indigenous bison species remain in Alaska today, although work is ongoing to re-establish wood bison (*Bison bison athabascae*) in the Innoko River region of southwest Alaska. However, in 1928, 22 plains bison (*Bison bison bison*) from the National Bison Range in Montana were introduced to the Delta Junction region, about 150 km southeast of Fairbanks, Alaska (Fig. 1). The bison quickly adapted to the riverine and upland ecotones along the Tanana and Delta Rivers, and by the 1950s, the population was estimated at several hundred individuals and could support limited sport hunting, as well as the establishment of herds in the Copper River (1950), Chitina (1962), and Farewell (1965, 1968) regions (Gipson and McKendrick, 1981; Coates, 1997; Paul, 2009). The Delta bison herd remains a healthy and viable population of 450–500 individuals, the largest of four plains bison herds in Alaska (Harper and McCarthy, 2014), but it is closely managed by

the Alaska Department of Fish and Game (ADF&G). The Alaskan *Bison bison bison* populations represent some of the few plains bison herds that have no genetic admixture with domesticated cattle (Paul, 2009). While the herd's behavior is heavily influenced and manipulated by human activity (e.g., Gipson and McKendrick, 1981; Paul, 2009), the herd is considered wild and free ranging and is well suited to test the reliability of these methods.

Seasonal Mobility Patterns

Because the Delta bison herd is closely monitored by the ADF&G, seasonal mobility patterns are well documented. The bison move between different ecotones on a seasonal basis, traveling an average total distance of approximately 250 km throughout the year between the Tanana and mid Delta River Valleys. Their habitat area encompasses approximately 2230 km^2, and the bison traverse an elevation gradient of ~300 m between summer and winter seasons. The seasonal mobility patterns of the herd are as follows (see also Fig. 1):

The winter range is the largest, encompassing more than 1500 km^2. The herd spends the longest time in the winter range, covering about six months from October through March. A majority of the herd spends the winter in the region north of the Granite Range, south of the Tanana River, east of Jarvis Creek, and west of the Gerstle River. The confluence of the Gerstle and Tanana Rivers, the outlet of Healy Lake, and the boggy areas near the headwaters of the Delta Clearwater River are particularly favored regions, and this preference may relate to the availability of open-water sources in that area during the winter.

In March, the herd begins to move south and then west to reach the primary spring calving grounds along the Delta River near Donnelly Dome. This spring migration covers approximately 50 km and passes through the fall mating grounds north of the Granite Range. Most calves are born in May; however, the time spent in the spring calving grounds is relatively short, only six to eight weeks. While most parturition occurs within the Delta River floodplain west and north of Donnelly Dome, some cows and neonates have been observed as far east as Jarvis Creek and as far south as Black Rapids Creek.

During the summer (June and July), the herd is dispersed throughout the Delta River basin, favoring gravel bars, vegetated outwash plains, and old glacial terraces along the river banks. The main herd distribution extends from approximately 12 km north of Donnelly Dome, throughout the Delta River basin and to Black Rapids Creek in the south, a distance of more than 50 km. Within the past decade, portions of the herd have been observed several miles west of the Delta River on upland terraces near Delta Creek. While the ADF&G has noted only relatively small differences between sexes in migratory behavior, solitary bulls have been observed in the Delta River/Jarvis Creek floodplain during the summer and in the Gerstle River floodplain in late summer and early fall.

During July and August, the herd migrates to the area between Jarvis Creek and the Gerstle River, approximately halfway between the summer and winter ranges, for the fall rut. The herd displays high fidelity to this mating area and congregates there for approximately one month before dispersing into the late fall range. The late fall and winter ranges are nearly identical, but the late fall range incorporates higher-elevation areas north of the foothills of the Granite Range, while the winter range incorporates lower-elevation areas along the Tanana and lower Gerstle Rivers.

It is worth noting that individual bison or small groups of adults have been observed in areas away from the rest of the main herd during different periods of the year. However, cows and calves typically congregate together to form a larger herd in these seasonal ranges, likely as security against predation (e.g., Plumb et al., 2014).

MATERIALS AND METHODS

Predicting $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ Variability

This study uses a high-resolution predictive model of $^{87}Sr/^{86}Sr$ values for Alaska that was generated by Bataille et al. (2014). This isoscape was created using a 1000 m Digital Elevation Model (DEM), which provides a map of the predicted values with much higher resolution than is typically incorporated into mobility studies and allows for fine-scale comparisons of the measured values. The isoscape was developed using best practices for modeling $^{87}Sr/^{86}Sr$ variability and was based on bedrock composition, geologic age, and ^{87}Rb chemical weathering for the geologic terrains in Alaska. Sub-models were developed and tested using Monte Carlo simulations. The resulting raster datasets from the sub-models were mosaicked to derive minimum, maximum, median, and first and third quartile models for $^{87}Sr/^{86}Sr$ variability across the entire surface of Alaska and these models were then validated using 885 rock and 339 water samples (Bataille et al., 2014).

Our study area was defined by a 50 km radius encompassing the Delta bison herd range (Fig. 2); data on $^{87}Sr/^{86}Sr$ values were extracted from the 3rd quartile raster dataset from Bataille et al. (2014) using ArcMap 10.2 software. Information compiled by the ADF&G over several decades regarding where the bison congregate during certain times of the year was then used to delineate seasonal bison ranges within the Bataille et al. (2014) data subset (Fig. 3). The predicted $^{87}Sr/^{86}Sr$ mean, minimum, and maximum values for each of the restricted ranges were then calculated to provide expectations for how $^{87}Sr/^{86}Sr$ values in the tooth profiles may vary seasonally (Table 1). The results indicate that the Delta bison herd home range is an excellent location to assess the reliability of these methods because the $^{87}Sr/^{86}Sr$ values vary widely for such a small area, on the scale of the third decimal.

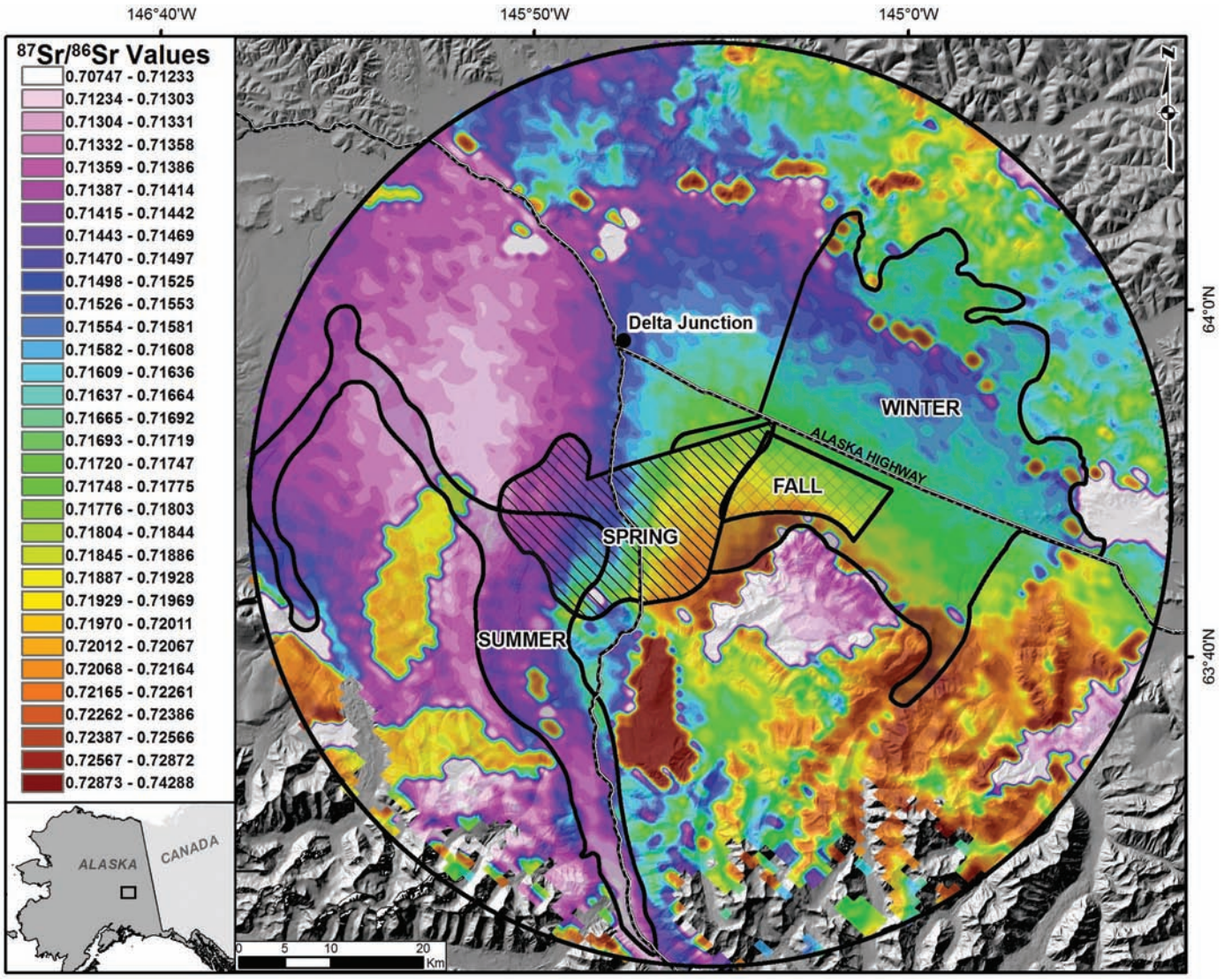

FIG. 2. $^{87}Sr/^{86}Sr$ isoscape for the Delta region. Predicted $^{87}Sr/^{86}Sr$ variation within a 50 km radius encompassing the Delta bison herd habitat area (derived from the Bataille et al., 2014 raster dataset).

We assume that the $^{87}Sr/^{86}Sr$ values in the teeth accurately reflect the bioavailable $^{87}Sr/^{86}Sr$ values in the areas where the bison were living during tooth formation. However, the bioavailable $^{87}Sr/^{86}Sr$ values in the study region may vary from the isoscape. While the isoscape predicted up to 80% of $^{87}Sr/^{86}Sr$ variability for certain rock types (Bataille et al., 2014), it has not been tested on any terrestrial species such as plants, small mammals, or snails (e.g., Maurer et al., 2012; Hartman and Richards, 2014), but see Padilla et al. (2015) for anadromous fish. However, we assume that the isoscape captures the bioavailable $^{87}Sr/^{86}Sr$ means for each of the seasonal habitat areas well enough to use for seasonal-level migration studies such as this one.

We also developed expectations for $\delta^{18}O$ variability, which were based on an isoscape for Alaska that was derived from $\delta^{18}O$ surface water values (Lachniet et al., 2016). The isoscape raster dataset indicated that the predicted range of $\delta^{18}O$ values for the area encompassing the Delta bison herd's habitat is between −20.2‰ and −30.2‰ (Fig. 4), relative to Vienna Standard Mean Ocean Water (VSMOW). Restricting the isoscape to just the seasonal habitat areas provides a much narrower range of $\delta^{18}O_{VSMOW}$ values, between −20.2‰ and −24.4‰, with a mean of −21.7‰ (Fig. 4). While this range of estimated values does not account for seasonal highs and lows, which likely include more extreme values, it provides an estimated amplitude of 4.2‰. The $\delta^{18}O$ values from bison tooth enamel carbonate and surface waters correlate well (Hoppe, 2006) and can provide expectations for the range of $\delta^{18}O$ values that should be displayed in the tooth enamel. Using equation 3 from Hoppe (2006:412), the mean $\delta^{18}O_{VSMOW}$ range for the Delta bison herd should be between 10.9‰ and 18.9‰. Converting the values to Vienna Pee Dee Belemnite (VPDB) following Coplen et al. (1983) provides a predicted range of $\delta^{18}O_{VPDB}$ between −11.7‰ and −19.4‰ and a seasonal amplitude of 4.1‰.

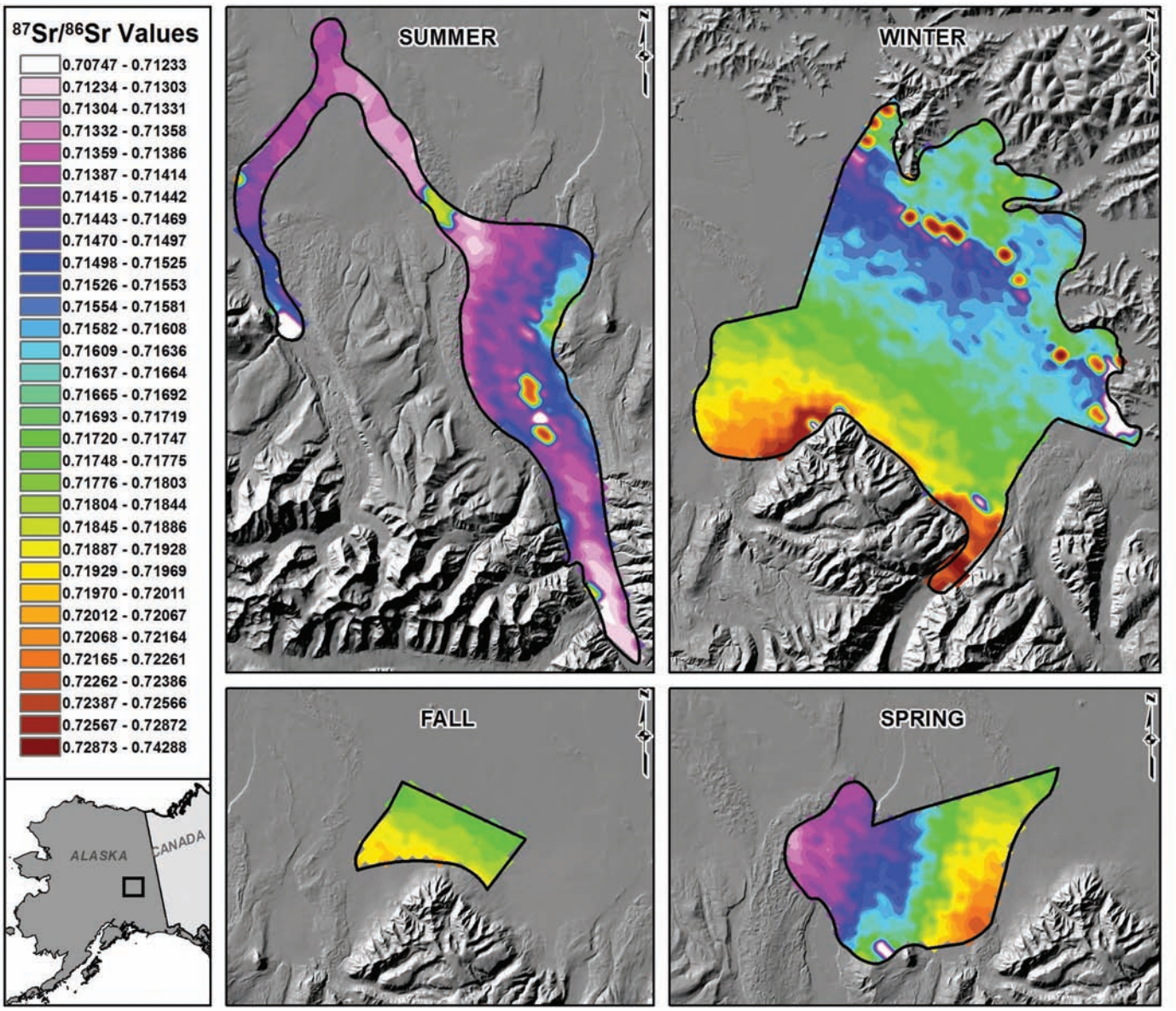

FIG. 3. Predicted $^{87}Sr/^{86}Sr$ variation in the seasonal habitat areas (derived from the Bataille et al., 2014 raster dataset).

TABLE 1. Predicted $^{87}Sr/^{86}Sr$ values for the seasonal habitats. The mean, standard deviation (SD), minimum, and maximum $^{87}Sr/^{86}Sr$ values are based on the Bataille et al. (2014) raster dataset. This variation is illustrated in an isoscape map in Figure 3. The amount of time spent in each seasonal habitat per year is listed as %Time.

Seasonal range	Area km^2	Duration	%Time	Mean	SD	Min	Max
Spring	361	6–8 weeks	13%	0.71671	0.00234	0.71051	0.72342
Summer	542	8–10 weeks	17%	0.71442	0.00155	0.70940	0.72390
Fall (Mating)	106	4–5 weeks	10%	0.71839	0.00076	0.71718	0.72080
Winter	1202	30–32 weeks	60%	0.71750	0.00260	0.71013	0.73144

Tooth Specimens

Three teeth were sampled for this study. The teeth were from two bison that were harvested during the 2012–13 Alaska Game Management Unit 20D bison hunting season and were collected by the ADF&G. The sex of the individuals was not recorded, but it is unnecessary for this study as male and female bison calves and juveniles have nearly identical behavioral patterns that mimic their mother's behavior (Plumb et al., 2014). Tooth wear indicated that the age of both individuals was four to six years, and all teeth showed slight wear at the apex. A lower second molar (M_2) and a lower third molar (M_3) were extracted from the first individual (DH1), and an M_3 was extracted from the second

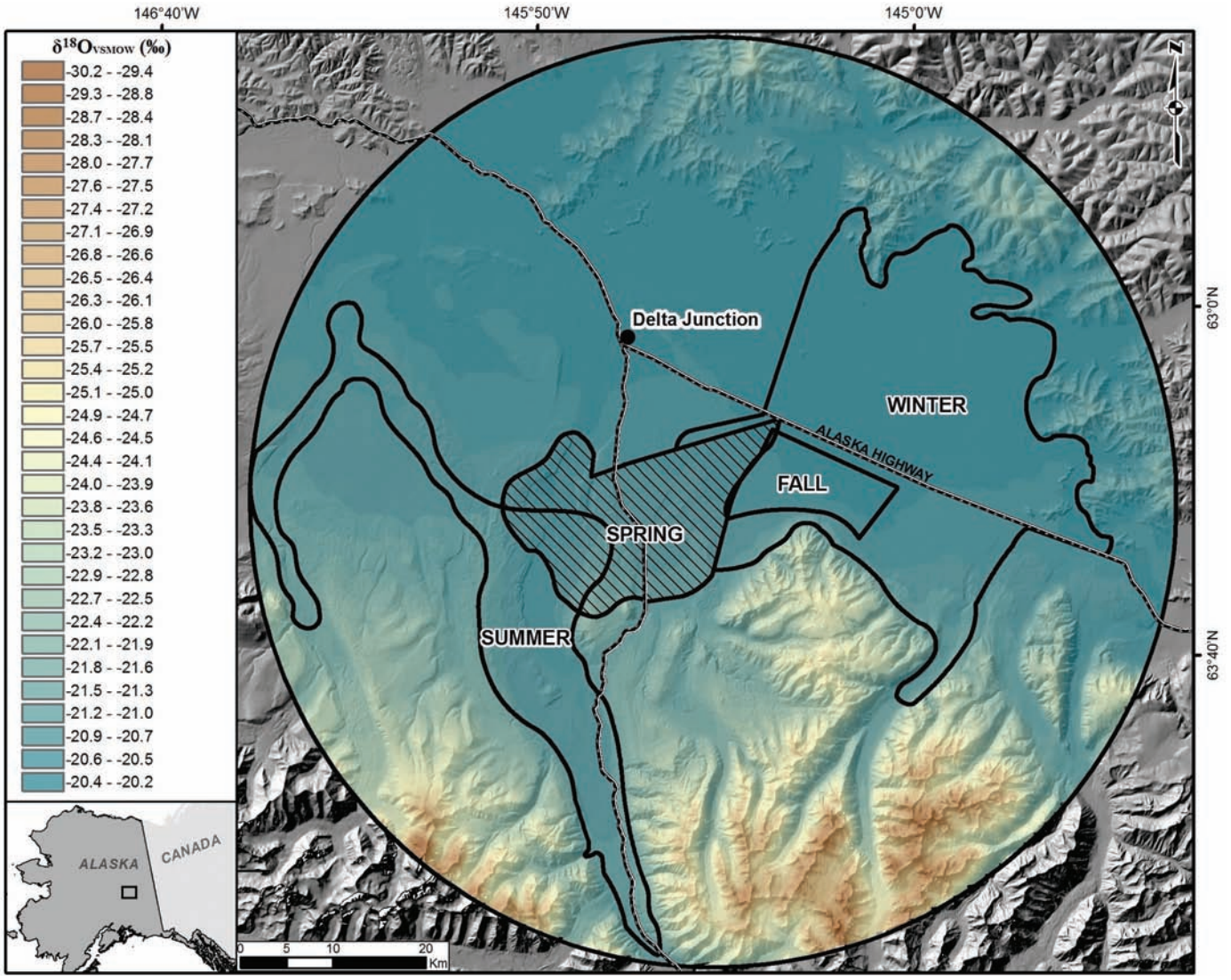

FIG. 4. Predicted $\delta^{18}O_{VSMOW}$ variation in the seasonal habitat areas (derived from the Lachniet et al., 2016 raster dataset).

individual (DH2). After extraction, the teeth were cleaned with dental picks, a sterile toothbrush, and deionized water and left to dry at room temperature for several days. After the specimens were dry, the surface of each tooth was abraded with a steel carbide bit using a handheld Dremel to remove approximately 0.05 to 0.10 mm of surface enamel that may have held particulate matter or contamination. After abrasion, each tooth was marked in 4 mm increments beginning at 2–3 mm above the cemento-enamel junction (CEJ) of the tooth. Samples of enamel weighing 50–60 g were collected by drilling out a 2–3 mm transect on the transverse plane of each tooth with a 1 mm diamond-coated bit. The samples for all three teeth were removed from the buccal side where the enamel is thicker (see Fig. 5). A total of 27 individual samples were collected from the three teeth.

Sample Preparation and Analysis

Laboratory methods were modified from Koch et al. (1997) and Widga et al. (2010), as described below. After the samples were removed from the teeth, 25 mg of powdered enamel was split off and prepared for stable oxygen isotope analysis by purifying and removing organic particulates in a 1 ml solution of 2% sodium hypochlorite (NaOCl) for 24 hours and rinsing three times with deionized water (centrifuging between rinses). Then a 1 ml solution of 1% acetic acid (CH_3CO_2H) was added for four hours, before the samples were again rinsed three times with deionized water (centrifuging between rinses) and then lyophilized for 24 hours. After completion of the chemical processing, 3–4 mg of each sample was weighed for analysis at the Alaska Stable Isotope Facility in the Water and Environmental Research Center at the University of Alaska Fairbanks. Stable isotope data were obtained using continuous-flow isotope ratio mass spectrometry (IRMS). The samples were analyzed on a Thermo Scientific GasBench II carbonate analyzer coupled with a DeltaV Isotope Ratio Mass Spectrometer. CO_2 was separated chromatographically from other gases present in the samples and then transferred to the IRMS, where the

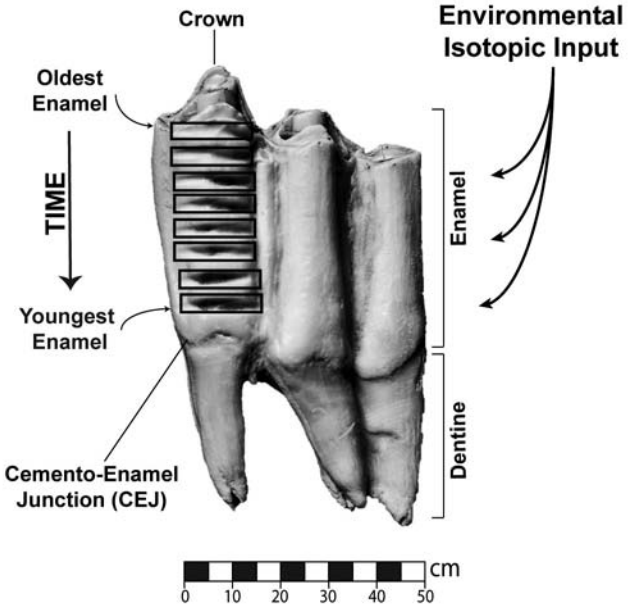

FIG. 5. Example of a sequentially sampled bison molar. Sample locations (black rectangles) are placed along the buccal side of an M_3. Ungulate teeth grow sequentially from crown to CEJ, allowing for multiple samples to be removed along the transverse plane of the tooth that can be associated with specific periods of growth.

oxygen stable isotopes were measured. Ten measurements were performed for each sample, and the mean and standard deviation of the 10 measurements were then calculated and reported. A blank sample was analyzed every 20 samples, and a laboratory standard (calcium carbonate) was analyzed every 10 samples. National Institute of Standards and Technology (NIST) standards REF-8543, 8544, and 8545 and International Atomic Energy Agency (IAEA) standards CO-8 and CO-9 were analyzed at the beginning of the sequence to ensure instrumentation calibration.

Additionally, 20 mg of each sample was sent to the Geochemistry Laboratory at the University of Utah in Salt Lake City to be chemically prepared and analyzed for $^{87}Sr/^{86}Sr$ values on a Thermo Scientific, High-Resolution Neptune (Bremen, Germany) Multicollector-Inductively Coupled Plasma Mass Spectrometer (MC-ICPMS). The University of Utah laboratory used a method that was developed there to purify strontium for the $^{87}Sr/^{86}Sr$ analysis via a system of introducing aqueous solution using an inline chromatographic column (see Mackey and Fernandez, 2011 and Brennan et al., 2014 for additional information on the purification process). Blanks or NIST standard reference material SRM987 were run between samples to ensure instrument calibration.

RESULTS

Predicted Seasonal $^{87}Sr/^{86}Sr$ Means

The $^{87}Sr/^{86}Sr$ isoscape published by Bataille et al. (2014) provided expectations about how $^{87}Sr/^{86}Sr$ values may vary across the seasonal bison ranges. As discussed, a 50 km subset containing the $^{87}Sr/^{86}Sr$ variation for the entire herd range was extracted from the raster dataset. The $^{87}Sr/^{86}Sr$ values predicted for this range vary between 0.70747 and 0.74288, with a mean of 0.71671 (Fig. 2). However, this predicted range includes highly localized areas (on the scale of < 5 km^2) with extreme values. If these extremes are excluded, the predicted range of $^{87}Sr/^{86}Sr$ values is restricted (0.71359 to 0.72011), with only a few localized regions with higher or lower values. These predicted values can be further restricted to the known seasonal habitat areas, which provides a much tighter range of values (Fig. 3, Table 1). The fall range, occupied for a short time during the mating season, has the highest mean at 0.71839, followed by the winter range at 0.71750. The spring range, occupied during the calving season, has a mean of 0.71671, followed by the summer range, which has the lowest mean at 0.71442. The predicted $^{87}Sr/^{86}Sr$ values for the seasonal ranges vary significantly for such small areas, with the summer and fall means varying by nearly 0.00400.

$^{87}Sr/^{86}Sr$ and $\delta^{18}O$ Results

The combined $^{87}Sr/^{86}Sr$ mean for all three teeth is 0.71607 (SD = ± 0.00043), falling well within the range predicted by the isoscape. The $^{87}Sr/^{86}Sr$ means for the individual teeth (Table 2) vary slightly, with the mean for DH1a (M_2) at 0.71583 (SD = ± 0.00033), DH1b (M_3) at 0.71590 (SD = ± 0.00035), and DH2 (M_3) at 0.71637 (SD = ± 0.00038). DH2 has the highest standard deviation (± 0.00038), but the samples from this tooth cover the longest period of growth. The lowest $^{87}Sr/^{86}Sr$ value is from sample DH1a-8 at 0.71525, while the highest $^{87}Sr/^{86}Sr$ value is from sample DH2-9 at 0.71711 (Table 3). Duplicate analysis was run on several samples (n = 13), with a resulting precision of ± 0.00002. The mean reported standard error is 0.00001 for all samples.

TABLE 2. Summary of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ results. The mean, standard deviation (SD), and range for the $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values are listed, along with amplitude (Amp.) for $\delta^{18}O$ values. #Samp lists the number of samples that were removed from that specimen. Standard deviation is determined from the specimen mean. Amplitude is the difference between the highest and lowest values for that specimen.

		$^{87}Sr/^{86}Sr$			$\delta^{18}O$ (‰)			
ID	#Samp	Mean	SD	Range	Mean	SD	Range	Amp.
DH1a	8	0.71583	0.00033	0.71523 to 0.71628	−18.7	1.2	−17.2 to −20.8	3.6
DH1b	8	0.71590	0.00035	0.71540 to 0.71635	−19.4	0.9	−18.6 to −20.8	2.7
DH2	11	0.71637	0.00038	0.71582 to 0.71714	−19.7	0.7	−18.5 to −20.6	2.1

TABLE 3. $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values and reported error. Strontium isotopes values were calibrated using SRM987. Oxygen isotopes values were reported relative to VPDB. Error values represent standard reported analytical error. Distance from CEJ is the distance from the cemento-enamel junction to the start of the sample location on the lateral margin of the tooth.

Sample ID	Distance from CEJ	$^{87}Sr/^{86}Sr$	Error $^{87}Sr/^{86}Sr$	$\delta^{18}O_{VPDB}$ (‰)	Error $\delta^{18}O_{VPDB}$ (‰)	$\delta^{18}O_{VSMOW}$ (‰)[1]
DH1a-1	31.2	0.71556	0.00002	−17.8	0.2	14.1
DH1a-2	27.2	0.71584	0.00002	−17.4	0.2	14.7
DH1a-3	23.2	0.71599	0.00001	−17.6	0.2	14.3
DH1a-4	19.3	0.71626	0.00002	−18.0	0.1	14.0
DH1a-5	15.6	0.71622	0.00002	−18.8	0.2	13.1
DH1a-6	11.8	0.71591	0.00002	−19.3	0.1	12.7
DH1a-7	8.3	0.71562	0.00002	−20.2	0.2	11.8
DH1a-8	3.7	0.71525	0.00002	−20.7	0.2	11.1
DH1b-1	33.7	0.71542	0.00002	−20.6	0.2	11.2
DH1b-2	30.1	0.71544	0.00002	−20.4	0.2	11.5
DH1b-3	25.7	0.71569	0.00002	−20.3	0.2	11.6
DH1b-4	21.5	0.71579	0.00002	−19.7	0.2	12.2
DH1b-5	17.0	0.71607	0.00002	−18.6	0.2	13.3
DH1b-6	13.7	0.71633	0.00002	−18.3	0.2	13.8
DH1b-7	8.7	0.71628	0.00002	−18.4	0.1	13.5
DH1b-8	4.4	0.71620	0.00002	−19.1	0.2	12.8
DH2-1	43.9	0.71612	0.00002	−19.6	0.2	12.4
DH2-2	39.3	0.71584	0.00002	−20.2	0.1	11.8
DH2-3	35.7	0.71608	0.00002	−20.5	0.1	11.3
DH2-4	31.3	0.71609	0.00001	−20.3	0.1	11.6
DH2-5	27.9	0.71617	0.00002	−20.3	0.2	11.7
DH2-6	23.6	0.71624	0.00002	−20.1	0.2	11.9
DH2-7	20.0	0.71642	0.00002	−19.3	0.1	12.6
DH2-8	16.5	0.71683	0.00002	−18.9	0.2	13.1
DH2-9	12.4	0.71711	0.00002	−18.7	0.2	13.4
DH2-10	7.8	0.71679	0.00002	−18.9	0.2	13.1
DH2-11	3.7	0.71639	0.00002	−20.0	0.2	12.0

[1] $\delta^{18}O_{VSMOW}$ values were derived using the conversion formula from Coplen et al. (1983).

The $\delta^{18}O$ values are reported relative to VPDB, with a mean reported standard deviation of 0.3‰. The combined mean for the $\delta^{18}O$ values for all three teeth is −19.3‰ (SD = ± 1.0‰). The individual means for the teeth are −18.7‰ (SD = ± 1.2) for DH1a, −19.4‰ (SD = ± 0.9) for DH1b, and −19.7‰ (SD = ± 0.7) for DH2. The mean $\delta^{18}O$ values, standard deviations, and ranges for the specimens are presented in Table 2. The mean $\delta^{18}O$ amplitude for the samples is 2.8‰. The amplitudes for the M_3s are similar; however, the amplitude for the M_2 is almost 1.0‰ higher than those of the M_3s at 3.6‰. The combined mean of the three teeth (−19.3‰) also falls within the range of values predicted by the isoscape (Lachniet et al., 2016). Using the conversion formula to compare surface water values with tooth enamel carbonate (Hoppe, 2006) yielded a predicted range of −11.7‰ to −19.4‰ for $\delta^{18}O_{VPDB}$ values. However, Clementz and Koch (2001) and Hoppe (2006) caution that $\delta^{18}O$ means should be derived only from samples of at least four individuals. Recognizing this limitation, we compared the $\delta^{18}O$ means only to obtain approximate values and see if they are similar, and these means are not discussed further.

Modeling Sample Locations

At maximum length, M_2s cover 11 months of growth and M_3s cover 15 months of growth; however, the teeth used in this study were slightly worn on the occlusal surface, which reduces the amount of time that is captured in the isotopic profiles. The M_2 from the first individual (DH1a) was 39.3 cm long (measured from occlusal surface to CEJ) representing an estimated 9–10 months of growth. The M_3 for the same individual (DH1b) was 46.6 cm long, representing an estimated 11–12 months. The M_3 extracted from the second bison (DH2) was 55.4 cm long and had only slight wear on the occlusal surface. The samples from this specimen are estimated to represent nearly the full period of growth at 14 months.

As discussed, there are two scales of time to consider for time-series profiles. One scale is the physical growth of the enamel, which can be associated with calendrical approximations, and the other is the mineralization process, which takes much longer and is generally less understood. However, the first scale, physical growth, can be used to correlate sample locations from different teeth on the basis of known growth rates. We modeled the samples from the three teeth relative to one another using the following linear growth formula:

$$C_D = \left(\frac{F_L - CEJ_{DST}}{D_R} \right) + (Z)$$

where C_D is the calendrical approximation corresponding to the sample location, F_L is the total length of the tooth, CEJ_{DST} is the distance from the sample location to the cemento-enamel junction, D_R is the daily rate of tooth

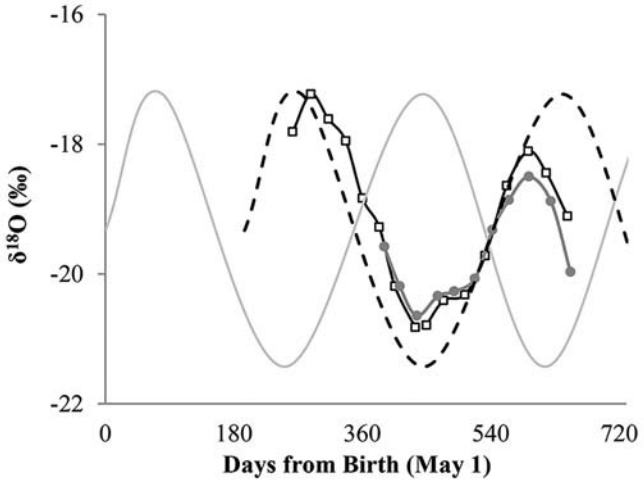

FIG. 6. Modeled sample locations and $\delta^{18}O$ values. The three $\delta^{18}O$ profiles closely align, based on the linear growth model (DH1: black line with white boxes; DH2: grey line with circles). The grey line represents the predicted $\delta^{18}O$ seasonal amplitude, assuming that our dataset captures 68.3% of the environmental variability. The dashed line shows the predicted seasonal $\delta^{18}O$ values shifted by 180 days.

growth, and *Z* is the number of days between birth and the beginning of tooth formation. For the model, we assume that birth occurs on 01 May, that M_2 total length is 63.4 mm, growth duration is 335 days, and formation begins on 01 July; and that M_3 total length is 67.8 mm, growth duration is 485 days, and formation begins on 01 February following birth (Gadbury et al., 2000; Passey and Cerling, 2002; Kohn, 2004; Widga, 2006). The results of the modeled sample locations (Fig. 6) show similar $\delta^{18}O$ values relative to sample location for the three teeth. While the variable inputs for this model are only an estimate from other populations, this model allows for the individual samples to be compared to one another.

DISCUSSION

Seasonal $\delta^{18}O$ Profiles

Seasonal signatures for the time-series profiles were determined from the $\delta^{18}O$ results (Fig. 6). The mean $\delta^{18}O$ amplitude (measured as the difference between peak high and low values) for the dataset is 2.8‰ (Table 2). However, this amplitude is lower than predicted by the Lachniet et al. (2016) isoscape (~4.1‰) and does not capture the full range of seasonal $\delta^{18}O$ extremes. This result is likely caused by attenuation during the mineralization process, and it suggests that the $\delta^{18}O$ profiles from the teeth capture approximately 68.3% of the $\delta^{18}O$ seasonal amplitude. Zazzo et al. (2012) found similar results for samples removed from the buccal side of domesticated sheep (*Ovis aries*) molars, which captured 64.9% of the seasonal $\delta^{18}O$ amplitude. These findings suggest that for the Bovidae family, $\delta^{18}O$ samples removed from the buccal side of molars capture between 60% and 70% of the environmental variability, but the percentage varies from species to species. Assuming the $\delta^{18}O$ dataset captures 68.3% of the seasonal amplitude, the estimated environmental $\delta^{18}O$ values are illustrated as the grey line in Figure 6, with the summer peak highs and winter peak low aligned on July 20 and January 20, respectively. While this range of values is higher than the mean range of values predicted by the Lachniet et al. (2016) isoscape, the isoscape provides only yearly mean $\delta^{18}O$ values and does not account for seasonal extremes or climate variability that may occur from year to year. However, as Figure 6 shows, the $\delta^{18}O$ profiles do not align with the predicted seasonal highs and lows and seem to be shifted by approximately six months (illustrated as the dashed line).

Numerous studies have indicated that the mineralization phase may take six or more months to complete, resulting in a homogenization of environmental isotope values (Balasse, 2002, 2003; Passey and Cerling, 2002; Hoppe et al., 2004; Kohn, 2004; Zazzo et al., 2005, 2012; Montgomery et al., 2010). The $\delta^{18}O$ profiles from the Delta herd specimens are consistent with this view, and if we shift the predicted $\delta^{18}O$ values by 180 days (dashed line in Fig. 6), the seasonal sinusoidal pattern corresponds well with the results. Factors other than attenuation, including the sampling methods, may also be causing this apparent shift in values. The samples were removed from the buccal side of the teeth where the enamel is the thickest. However, this choice increased the chance of bisecting multiple multi-directional enamel layers during the sampling process—layers that mineralize at different times (Suga et al., 1970; Suga, 1982; Zazzo et al., 2012). This bisection could likely lead to great attenuation of the isotope values. The linear growth model also assumes that summer and winter peak $\delta^{18}O$ values will occur every six months. In reality, the summer season in Alaska is much shorter than the winter season. The $\delta^{18}O$ profiles show this by the wider angle of the winter curve and tighter angles of the summer curves. This pattern may also result from the reduction of the enamel growth rate towards the end of the crown. A non-linear rate of growth that decreases with age would explain the slight offset of the M_3 profiles during the second summer (e.g., Zazzo et al., 2012; Bendry et al., 2015).

Predicted vs. Measured $^{87}Sr/^{86}Sr$ Signatures

The seasonal $\delta^{18}O$ signatures (Fig. 6) were used to match up the summer and winter seasons for the $^{87}Sr/^{86}Sr$ results (Fig. 7). The seasonal profiles generally matched the expectations for the seasonal $^{87}Sr/^{86}Sr$ signatures. The predicted $^{87}Sr/^{86}Sr$ mean, minimum, maximum, and SD values for each of the seasonal ranges (Fig. 3, Table 1) were also compared to the measured values in the bison teeth. The fall mating range—which is occupied by the herd for the shortest duration, approximately four weeks in late July and August—has the highest $^{87}Sr/^{86}Sr$ mean at 0.71839, followed by the winter range, which is occupied from September

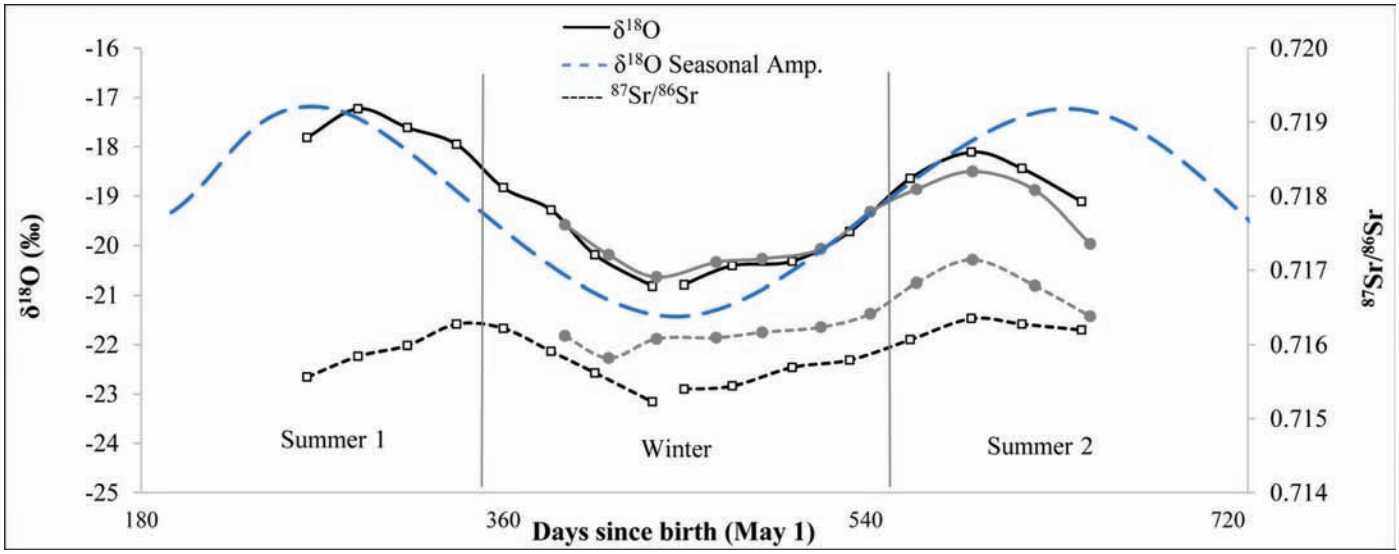

FIG. 7. Comparison of $\delta^{18}O$ seasons and $^{87}Sr/^{86}Sr$ values. The $\delta^{18}O$ peak high and low values were used to align with the $^{87}Sr/^{86}Sr$ values (DH1: black line with white boxes; DH2: grey line with circles). Summer and winter determinations were based on the $\delta^{18}O$ seasonal amplitude (dashed blue line).

through March and has a mean of 0.71750. The spring range, occupied during the calving season for approximately six to eight weeks between late April and early June, has a mean value of 0.71671, followed by the summer range, which is occupied during June and July, and has the lowest mean at 0.71442. The yearly pattern for the $^{87}Sr/^{86}Sr$ profiles expected from these means would begin with relatively low values (the spring/summer signature), increase for a short period (the fall signature), and then decrease slightly and remain steady for a long period (the winter signature). However, attenuation during the mineralization phase can skew these signatures, leading to less pronounced changes in the seasonal profiles.

While the predicted fall signature suggests there should be a small spike in $^{87}Sr/^{86}Sr$ values for the profile, this spike may not be apparent in the results because of the short time (10% of the year) that the bison spend in the fall habitat area. Additionally, the predicted $^{87}Sr/^{86}Sr$ values for all of the seasonal habitat areas except the fall range have a high standard deviation (see Table 2). Another complication is that individual bison can have migratory behavior that occasionally deviates from the general seasonal pattern of the herd, and there is no way to know whether the bison in this study showed fidelity to the general herd patterns. However, cows with calves and juveniles (i.e., the demographic of our dataset during the period the teeth were forming) have the highest herd fidelity. Another reason the measured values might vary from the predicted signatures is that bioavailable $^{87}Sr/^{86}Sr$, especially in large watersheds like the Tanana and Delta Rivers, can vary significantly because sediments are transported and deposited from many different sources. This transport and deposition can result in $^{87}Sr/^{86}Sr$ signatures for watersheds that differ from surrounding $^{87}Sr/^{86}Sr$ soil values.

However, despite these potential complications, the $^{87}Sr/^{86}Sr$ profiles for both individuals (Fig. 7) appear to match the predicted seasonal pattern and, with the exception of one sample (DH1a-8), fall within the range of values for the seasonal habitat areas. The dashed line in Figure 8 represents the predicted seasonal values relative to the duration of time spent in each of the habitat areas (spring: 13%, summer: 17%, fall: 10%, and winter: 60%). The SD for each of the seasonal habitat areas is represented by error bars and shows that most of the values in the tooth profiles also fall within the SD for each of the seasonal areas. The profile for the second spring/summer shows higher-than-predicted values, which may reflect the movement of the bison south and west along the base of the Granite Range to reach their spring calving grounds. The Granite Range region has much higher $^{87}Sr/^{86}Sr$ values than either the winter or the spring range (Fig. 3). The winter profile also shows an unexpected decrease in values that did not match the means from the isoscape. This decrease could be a result of the bison's inhabiting a more restricted area during the winter, such as the boggy region between the Tanana and Delta Clearwater Rivers. That area is a favored wintering spot for the Delta herd, and a significant portion of the herd typically congregates there for several weeks or months during midwinter. This area has $^{87}Sr/^{86}Sr$ values lower than the predicted mean for the winter range, which would result in a lower $^{87}Sr/^{86}Sr$ winter signature in the seasonal profiles (see Fig. 3). Even considering the variation between the predicted and measured signatures, the $^{87}Sr/^{86}Sr$ values track well with known seasonal mobility patterns for the Delta bison herd, falling well within the predicted range of values for the seasonal habitat areas.

Douglas et al. (2013) indicated that $^{87}Sr/^{86}Sr$ values can vary in hydrological systems in interior Alaska as a result of seasonal temperature, precipitation, and permafrost dynamics and could potentially confound mobility studies in high-latitude regions. However, seasonal fluctuations in $^{87}Sr/^{86}Sr$ values due to the freeze-thaw cycle do not seem to have affected the results. Our results show that the seasonal

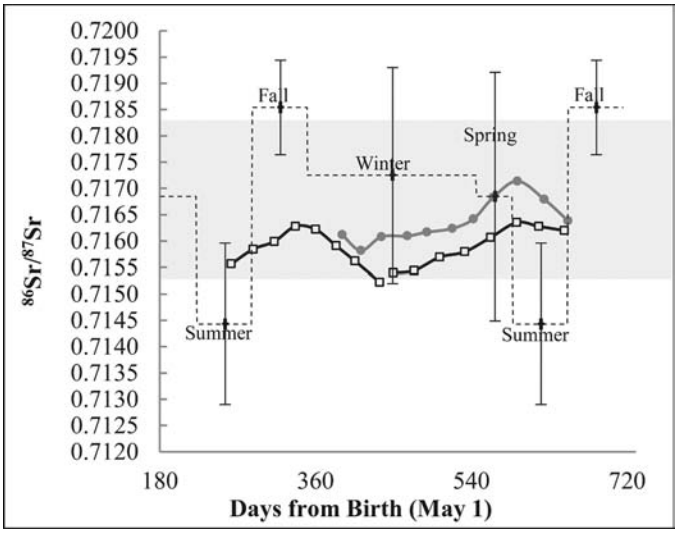

FIG. 8. Modeled sample locations and $^{87}Sr/^{86}Sr$ values. $^{87}Sr/^{86}Sr$ profiles plotted on the basis of the linear growth model (DH1: black line with white boxes; DH2: grey line with circles). The dashed line represents the mean $^{87}Sr/^{86}Sr$ value for each seasonal habitat area, relative to the duration of time spent in each area. The shaded area represents the $^{87}Sr/^{86}Sr$ mean of the four seasonal areas ± SD. The error bars represent the $^{87}Sr/^{86}Sr$ SD for each of the seasonal areas.

pattern of $^{87}Sr/^{86}Sr$ values for the three bison teeth track with the known seasonal migration patterns of the herd. The $^{87}Sr/^{86}Sr$ profiles fell well within the predicted range for the seasonal habitat areas, which suggests that the sinusoidal pattern in the $^{87}Sr/^{86}Sr$ profiles results from movement across the landscape, rather than from fluctuations in the bioavailable $^{87}Sr/^{86}Sr$. Our results indicate that these methods are reliable for reconstructing bison mobility patterns in a high-latitude region and could also be used for reconstructing prehistoric mobility patterns in similar environments.

This study also demonstrates that attenuation during the mineralization process is a confounding issue for tracking or interpreting seasonal signatures. In regions with more homogenous $^{87}Sr/^{86}Sr$ values, it would likely be difficult to tease out individual seasonal signatures because small changes in the $^{87}Sr/^{86}Sr$ values would be smoothed out. Studies that use similar methods should ensure that the study region has large enough differences in $^{87}Sr/^{86}Sr$ values that the seasonal signatures would not be obscured by attenuation. This factor is also demonstrated by Britton (2009). Additionally, without knowing where the seasonal bison habitat areas were located for this study, or the duration of time the bison spent in each area, it would have been difficult to correlate the $^{87}Sr/^{86}Sr$ profiles with the correct physical locations on the landscape. While these methods are reliable for reconstructing broad-scale patterns of seasonal mobility for large migratory species, caution should be used when attempting to identify small-scale, seasonally occupied habitat areas on the basis of the isotope profiles alone. Future research efforts should also be directed at establishing the rate at which $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values are mineralized in bison tooth enamel. This type of research would be better addressed through studies with captive animals and controlled feeding experiments, rather than with free-ranging bison. However, at this stage, the number of controlled studies concerning $^{87}Sr/^{86}Sr$ isotopes in mammals is limited, emphasizing the value of our current investigation.

CONCLUSION

This pilot study investigated the use of time-series profiles of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ values as a proxy for reconstructing the seasonal mobility patterns of bison living in a high-latitude environment. The analysis of three sequentially sampled bison molars from two individuals of the Delta bison herd indicates that the methods are reliable on a broad seasonal scale and that the $^{87}Sr/^{86}Sr$ values track well with the known seasonal mobility behavior of the herd. On the basis of these results, we expect that these methods should also be reliable for reconstructing seasonal mobility patterns of prehistoric bison. This conclusion has important implications for our understanding of past animal behavioral ecology, and future work applying these methods to prehistoric animals could potentially shed light on spatial and temporal ecosystem dynamics that would be difficult to investigate by other means. These methods can be especially valuable for understanding how animal behavioral ecology may have changed during periods of environmental stress. Alaska and the surrounding circumpolar regions have high densities of mammalian remains dating to the Pleistocene and early Holocene (e.g., Harington, 2003; Guthrie, 2006), and reconstructing animal behavioral ecology during these periods may be informative for understanding how modern circumpolar species could react to continued climate change in the future.

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